BOOK REVIEW: INSECTS FOR ALL SEASONS

TAUBER, M.J., C.A. TAUBER AND S. MASAKI. 1986. *Seasonal Adaptations of Insects.* Oxford University Press, New York. 411 pages, 16 text figures, bibliography, author index, species index, subject index. Price $39.95 USA.

When I consider writing up an investigation somewhat removed from the area of my most recent endeavor, I begin by reading a book that reviews the general topic. I have two main objectives: (1) to increase confidence about my grasp of the literature, and (2) to help forge a more synthetic entomological backbone for the paper that I would like to write. With these goals in mind, I purchased *Seasonal Adaptations of Insects* off the shelf in Blackwell's Bookstore, despite its scandalous British price. The book did not offer immediate help with either of my objectives, but instead laid bare the breadth of my ignorance about an important and interesting field of entomological research. The treatment is well organized and solidly documented with meaty discussions of work relevant to all major groups of insects. It is an excellent synthetic synopsis of a complex literature that has grown by leaps and bounds during the past 15 years. The authors lead the reader to delight in, rather than despair over, the incredible variety of phenological adaptations in insects, and suggest the outlines for a more holistic approach to empirical studies of insect life cycles. After reading the book, I share the authors' enthusiastic optimism about the future of such work. I also think that I got my money's worth!

The first five chapters provide a basis for understanding seasonal adaptations in the context of the "diapause syndrome". Chapter 1 provides a brief but useful historical summary about work on insect life cycles and clearly focuses the reader on the authors' two main objectives: (1) to describe the variety of seasonal adaptations employed by insects, and (2) to provide a synthetic basis for ecological and evolutionary studies of diapause. Chapter 2 provides a classification of the ways that insects respond to seasonal change and places diapause within a broader adaptive context. Chapter 3 describes the course of diapause with reference to the endless variations known among insects.

The fourth chapter is the keystone of the book, laying out the authors' concept of diapause. Their "diapause syndrome" is a more global and dynamic concept than those that are generally employed, and I found it more satisfying. For Tauber, Tauber and Masaki, diapause is not primarily concerned with surviving adverse conditions, but instead, with effecting broadly adaptive synchrony between insect population dynamics and seasonal variation in the environment, both biotic and abiotic. In their view then, the anticipatory nature of diapause is paramount, and seasonal synchronization is linked explicitly to neurohormonal bases. This broad concept removes any possible confusion between dormancy and diapause, isolates the evolution and development of cold hardiness as a parallel problem, and incorporates dormancy, migration and various polymorphisms in the adaptive context of the entire life cycle.

Chapter 5 is a brief but effective summary of how environment regulates seasonal cycles. Evidence for the central position of photoperiod in many species is crisply summarized, the primary inductive and secondary modifying effects of temperature are discussed, and these are considered in relation to other environmental characteristics known to influence the manifestation of diapause. The basis for constructing photoperiod response curves and for the concept of critical photoperiod are critically reviewed. Although the authors show that substantial progress has been made by assessing responses to static photoperiods, they argue that we must adopt a more dynamic approach in order to get crucial information about

diapause intensity, and in order to understand the effects of changing daylengths experienced by natural populations. The chapter is an excellent guide to the important primary literature, and work about groups that I know well was efficiently and accurately abstracted.

In Chapter 6, the authors explicitly tackle the vast diversity of insect life cycles by extending the general principles summarized in the first part of the book to insects of highly specialized adaptive zones or extreme habitats. The section about parasitoids underscores the diverse range of ways that the insect-parasitoid relationship can affect the life cycles of either partner. We also learn about how the unique aspects of social life are tied up in regulation of phenology among the social Hymenoptera. Unfortunately, there is only a passing descriptive reference to one paper about termites, and uncharacteristically, the authors do not mention whether more extensive information is available. The treatment of diapause in tropical insects is fascinating. Two important points are well established: (1) numerous tropical species show diapause, and (2) diapause is clearly adaptive in at least some tropical populations and not simply a result of introgression from more temperate populations. The chapter concludes with treatments of phenology in desert and arctic insects. Diapause is an important component of life in such environments and the diapause syndrome of arctic and desert species has been molded in weird and wonderous ways. However, as the authors point out, we have much to learn about the details of insect life cycles in both environments.

Chapters 7–9 consider the diapause syndrome as an evolutionary phenomenon. In Chapter 7, the authors partition genetic variation for seasonal adaptation into continuous variation in quantitative traits and disjunct variation in qualitative traits. They offer solid arguments about the fitness implications of quantitative traits such as intrapopulation variation of critical photoperiod, but also show that some variation has little direct relation to fitness and may have little adaptive value. They provide general guidelines for working out the genetics of diapause and document them with reviews of information now available. It appears that most quantitative traits are under polygenic control with genetic diversity maintained by variable selection pressures and intrapopulation genetic exchange. The relative importance of particular diversity maintaining processes are still a matter of dispute and may likely vary among taxa. Although Mendelian inheritance has been shown in only a few insect taxa where seasonal traits vary discretely, the authors believe that this will become more common as more detailed studies are made. The authors also discuss how genetic variation in polygenic traits can lead to polymorphisms with the incorporation of a threshold mechanism allowing continuous variation to be expressed discretely. This chapter provides a good starting place for anyone contemplating an evolutionary study of insect life cycles.

Chapter 8 provides an evolutionary scenario for diapause that links the diverse seasonal adaptations summarized in the earlier chapters and explains their control by a host of seasonal token stimuli. This general model allows for the obvious multiple evolution of diapause in the context of three steps. First, the authors assume the evolution of a time measuring system of some sort. The authors review the several models that have been published and show that there is still more to learn before we can make an informed choice among them. Second, their scenario requires the evolution of environmentally controlled neuroendocrinological responses in an adaptive context. The third stage involves the coupling of the neuroendocrine responses to seasonal environmental stimuli. The authors go on to show how their scheme provides a useful way of thinking about the evidence for evolution of diapause that has accumulated from studies employing artificial selection, work about colonizing species, and a host of comparative studies. In an illuminating critical discussion, they outline the benefits and limitations of the sorts of

broad comparative studies that have been made, and finish with a plea for detailed comparisons of environmental and physiological control mechanisms in groups of related species with well established phylogenies. This approach can reveal the polarity of diapause evolution in specific lineages. A simple, but yet instructive example is provided by discussion of the Taubers' own work with green lacewings in the *Chrysopa carnea* species complex.

The general evolution of life histories is viewed in the context of seasonal adaption in Chapter 9. Up to now most studies of insect life history have considered isolated features or suites of characters that are obviously co-adapted. Their diapause syndrome concept underscores that adaptation to seasonality influences life cycle timing and many other features of insect life history, and the authors rightly urge us to take a broader view of life history evolution in insects. Two important proximate objectives are readily accessible. First, we need to understand the limits of genetic variation for life history traits and relate the pattern of such variation to environmental correlates such as are envisioned by Southwood's (1977, *J. Anim. Ecol.* 46:337–365) notion of the "habitat templet". Genetic variation for life history has obvious geographical correlates and these are outlined in the context of a few well reviewed studies. Geographical variation in life cycles may also be related to speciation in many taxa. Second, we can search for pattern in how life history traits evolve together in the context of seasonality with particular attention to how fitness tradeoffs are managed by natural selection. Life cycles are indeed adaptive, but they are also constrained by their underlying genetic systems. We need to know more about how variation for life history traits is maintained before we can make progress toward this objective The final chapter effectively discharges the entomologist's standard social obligation by showing how understanding of life cycles is crucial to pest management. It is largely a summary of current applications and a discussion of several approaches that are under development now. There is not much new information or conceptual synthesis useful to pest managers. However, for those desiring a summary of the anthorpocentric justification for studying insect life cycles, the chapter will be useful. It is ideal reading for intoductory students in pest management and I will use it in my own teaching.

The book may be criticized because it largely ignores developments in the trendy literature of life history evolution. However, such criticism would miss the point. The authors and most entomologists are compelled by both interest and practical necessity to explain both highly complex life cycles and more life history variation than fits comfortably into general theoretical frameworks that have been developed to date. This book clearly establishes that life history variation within insect species, and often within populations, is as important as general patterns at higher taxonomic levels. Understanding how such variation is maintained and distributed geographically and taxonomically can become a major unifying theme in future work about insect life history.

The book is carefully written and produced. It is admirable for its clarity and scarcity of typographical error. Each chapter section is clearly summarized and this is very handy for both preview and review. The bibliography is immense, including nearly 2000 entries, most of which are cited in constructive arguments in the text. The indicies are superb and will make the book valuable as a reference on any entomological bookshelf. *Seasonal Adaptions of Insects* is a perfect basis for graduate seminar courses, and for allowing professional entomologists to catch up on an exploding literature.

Although the book confronts complexity squarely and without apology, the organization and presentation of material makes it easily digestible. Of the two objectives mentioned in the introductory chapter, the authors clearly succeed with the first; the complexities of insect life

history are superbly described and well documented. They light the way for an assault on the second objective by urging researchers to consider the genetic basis of insect life history, and to view life history in the more holistic context of the diapause syndrome. It is fair to point out that this task was begun by collections of authors at the last few International Congresses of Entomology [Dingle, H. (ed.), 1978, *Evolution of Insect Migragion and Diapause,* Springer-Verlag; Brown, V.K. and I. Hodek (eds.), 1983, *Diapause and Life Cycle Strategies in Insects.* Junk]. However, Tauber, Tauber and Masaki's new book is the first attempt to review the relations between insect life history and seasonality within a general entomological framework. Their book is highly successful and entomologists of all persuasions will profit from reading it. I hope that it will be widely read, and trust that it will inspire attention to the many fascinating problems that it raises.

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